2015

The Effects of Interspecific Interactions on the Reproductive Success of Carolina Chickadees (Poecile carolinensis)

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The Effects of Interspecific Interactions on the Reproductive Success of Carolina Chickadees (*Poecile carolinensis*)

by

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A Thesis

Presented to the Graduate and Research Committee

of Lehigh University

in Candidacy for the Degree of

Master of Science

In

Earth & Environmental Science

Lehigh University

May 2015

Thesis is accepted and approved in partial fulfillment of the requirements for the Master of Science in Earth & Environmental Science

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Acknowledgements

I would like to thank the many people that have helped me along the way. Students in both the ecology and biology labs were instrumental in completing this thesis. Thank you especially to Mike McQuillan, Ian Kelleher, and Joe Rozek for help with field and lab work. My advisors, Amber Rice and Robert Booth, were essential to my success with their many hours of guidance and support. In addition, I would like to thank Bruce Hargreaves for serving on my committee and providing plenty of helpful feedback. Furthermore, thank you to the American Museum of Natural History and The Smithsonian National Museum of Natural History for generously providing tissue samples for microsatellite analysis. Funding for this research was provided by the Lehigh University Earth & Environmental Science Department. Finally, I know this project would not have been possible without the support of my family and friends.

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Abstract:

The Carolina chickadee (*Poecile carolinensis*) is an ideal model organism to study how interspecific interactions collectively influence fitness in a dynamic environment because the species currently hybridizes with black-capped chickadees (*P. atricapillus*), competes with other bird species for nesting sites, and suffers from a variety of blood parasites. I investigated how multiple interspecific interactions cumulatively affect the reproductive success of Carolina chickadees along its northern range margin. I monitored chickadees in Pennsylvania to determine breeding success, blood parasite incidence, and hybridization, while investigating potential environmental correlates. Competition with house wrens (*Troglodytes aedon*) had the biggest impact on reproduction, destroying 33% of nests. Presence of blood parasites reduced chick condition, but did not appear to influence adults. No evidence of hybridization with black-capped chickadees was found, although previous research has reported hybridization nearby. Understanding the cumulative effects of interspecific interactions will facilitate improved predictions of ecological responses to changes in climate.

Introduction:

Earth's climate is rapidly changing and understanding how species will respond to these changes is a critical challenge for ecologists (Chen *et al* 2011, Dawson *et al* 2011). Biodiversity has been declining at a rapid rate for the past century, and the rate of loss will likely increase in response to climate change and other global changes (Butchart *et al* 2010). In addition, anticipated climatic changes of the coming decades and century are expected to lead to distribution and phenological shifts in many species (Sala *et al* 2000,

Parmesan 2006, Williams *et al* 2007, Chen *et al* 2011, Auer & Martin 2013). With changing distributions and phenologies, species that previously did not interact will be forced to share habitat, and they will begin to interact in new ways (Thomas *et al* 2004, Williams *et al* 2007, Harmon & Barton 2013). Understanding how interspecific interactions will be influenced by rapidly changing environments is critically needed to better anticipate changes in ecological communities and the ecosystems they support (Hoffman & Sgrò 2011). Baseline observational evidence describing the environmental sensitivity of interspecific interactions, and how these influence fitness, is needed for a variety of species, particularly along range margins where biotic responses to climate change may be greatest (Lavergne *et al* 2010, Dawson *et al* 2011).

Species interactions have already been influenced by climatic changes of the past few decades, oftentimes with surprising results (Zanette *et al* 2003, Parmesan 2006, Hoffman & Sgrò 2011). For example, in Arizona, lower amounts of winter snowpack have allowed elk greater access to vegetation throughout the winter, damaging trees; elk-induced vegetation changes have, in turn, forced multiple species of warblers to experience nest overlap. Nesting overlap is causing a reduction in reproductive success due to increased competition and predatory stress (Auer & Martin 2013). In Great Britain, newts have been entering ponds earlier in the spring than frogs in the last two decades, resulting in higher predation rates on tadpoles (Walther *et al* 2002). In short, it is important to understand how these sorts of interactions will be influenced further by climate change (Lavergne *et al* 2010, Şekercioğlu *et al* 2012). Therefore, in order to more fully understand and anticipate the ecological impacts of global climate change,

research is needed to describe and quantify the fitness effects of interspecific interactions, and how these interactions may be affected by environmental change.

The Carolina chickadee (*Poecile carolinensis*) is an ideal model organism to study how interspecific interactions collectively influence fitness in a dynamic environment. Carolina chickadees are small, residential songbirds found in deciduous forests in southern and mid-eastern North America (Brewer 1963, Kammermeier & Kelling 1999). They are currently moving northward with warming temperatures (Taylor *et a*l 2014a), and they experience a range of different interspecific interactions including hybridization, competition, and parasitism. Additionally, it is expected that the Carolina chickadee range will continue moving northward in the coming years (McQuillan & Rice *in review*), yet how this movement may influence hybridization, competition, and blood parasitism is unknown.

The Carolina chickadee has been found to hybridize with the closely related black-capped chickadee (*P. atricapillus*), which has a more northerly distribution (Fig. 1). Black-capped chickadees are extremely similar to Carolina chickadees in many respects including appearance, life history, and vocal calls (Brewer 1963). They are considered a sister species that likely diverged about 2.5 million years ago (Gill *et al* 2005, Harris *et al* 2014). The two species have a contact zone that runs east to west between their ranges, extending from New Jersey to Kansas, and hybridization within this zone has been documented by multiple sources (Brewer 1963, Merritt 1981, Reudink *et al* 2007, Taylor *et al* 2014a) (Fig. 1). Evidence suggests that hybrids in the Ohio portion of the hybrid zone have lower fitness than both parent species, especially when it comes to hatching and fledging success (Bronson *et al* 2003). Even though reduced fitness of

chickadee hybrids has been observed in a portion of the hybridization zone, it is not yet known how geographically extensive this observation is and its detrimental effects have not yet been quantified. With continuing climate change, it is expected that the Carolina chickadees will continue their movement northward into the black-capped range (Taylor *et al* 2014a, McQuillan and Rice *in review*), making it particularly important to understand the effects of hybridization on fitness. The hybrid zone has already moved eleven kilometers over the past ten years, which is consistent with juvenile dispersal rates (Taylor *et al* 2014b).

In addition to competiting with black-capped chickadees for mates, nesting sites, and food, Carolina chickadees must also compete with the house wren (*Trogodytes aedon*) (Doherty Jr. & Grubb Jr. 2002). The house wren is a migratory bird of similar size that relentlessly competes with chickadees or other birds and is often able to displace chickadee nests. House wrens may be destroying other species' nests to gain sites for themselves or to reduce food competition. Even after eggs are laid or chicks are hatched, chickadee nests are still vulnerable to takeover by house wrens since they peck at the eggs and small hatchlings to kill and remove them from nests (White & Kennedy 1997). House wrens tend to prefer forest edges to interiors, and habitat fragmentation and land-use changes have likely resulted in increases in wren populations (Doherty Jr. & Grubb Jr. 2002, Butchart *et al* 2010).

Carolina chickadees also experience parasitism. Blood parasites have been documented in Carolina chickadees, but it is not yet known how detrimental their effects may be in terms of reproductive success and fitness (Kirkpatrick & Suthers 1988, Collins *et al* 1966, Garvin & Remsen 1997). Bloodborne parasites are detrimental to their hosts

because they live off of its resources (Webb *et al* 2005, Elahi *et al* 2014). Furthermore, any immune responses of the host to defend against these parasites will result in decreased resource allocation to other activities, such as foraging or reproduction (Allander 1997, Knowles *et al* 2009, Barnard *et al* 2010, Krams *et al* 2013). In great reed warblers, higher parasite load was correlated with lower fledging success, further indicating that parasites can play an important role in fitness (DeGroote & Rodewald 2008, Asghar *et al* 2011). Furthermore, the threat of bloodborne parasites is expected to increase with global change due to increases in vector prevalence (Walther *et al* 2002, Parmesan 2006, Murdock *et al* 2013).

In this study, I investigated how the interactions of hybridization, competition, and blood parasitism cumulatively affect the reproductive success of the Carolina chickadee at sites along its northern range margin. To explore the effects that interspecific interactions have on the breeding success of Carolina chickadees, I monitored and captured breeding individuals to determine their reproductive success, genetic ancestry, and blood parasite levels. I also investigated differences in habitat characteristics among nest sites, to identify ecological correlates associated with fitness.

Methods:

Study Sites

Artificial nests were monitored across two growing seasons. For the 2013 season, chickadees nesting in artificial snags were monitored in two different sites: South Mountain (40°36'00.693" N, 75°21'54.985" W) and DeSales University (40°32'30.125" N, 75°22'45.244" W). For the 2014 season, I set up additional snags in these locations,

as well as new study sites at Nockamixon State Park (40°25'49.050" N, 75°14'55.484" W) and Peace Valley Park (40°20'17.474" N, 75°10'13.961" W) (Appendix I). These sites were relatively undisturbed, contained high-quality habitat for chickadee nesting, and formed a latitudinal transect across the presumed location of the chickadee hybrid zone in eastern Pennsylvania (Taylor *et al* 2014a). In addition to these sample sites, I measured and collected blood samples from chickadees captured during the winter at Jacobsburg State Park (40°47'03.993" N, 75°17'34.588" W), to use in the genetic ancestry analyses (Fig. 2).

Bird Capture and Nest Site Monitoring

I estimated reproductive success by observing birds breeding in the artificial nest snags set out in our four study sites (Fig. 2). The artificial snags were made out of 4-inch diameter polyvinyl chloride pipes that stood 1.3-meters high, modified from the design of Grubb & Bronson (1995).

All snags were monitored approximately every other day, starting in late April, to determine the dates when nests were started and the egg laying began. I recorded the number of eggs laid by each breeding female, and continued to monitor each active nest to determine the date of hatching. In addition, I also recorded if and when house wrens overtook nests that were started by chickadees. Chickadees lay four to nine eggs per clutch, and hatching is relatively synchronous, such that all viable eggs in a nest hatch within approximately a 24-hour period (Smith 1991). When the juveniles were ten days old, I captured the adults with mist nets set up in front of the entrance to each snag, and directly removed the juveniles from their nests. All birds were banded with individually

numbered aluminum bands provided by the United States Geological Survey (USGS), and had a small blood sample taken using brachial vein puncture (Owen 2011). I measured tail length, un-flattened wing chord length, tarsus length, and bill length for each adult, and only tarsus length in juveniles. The mass of each bird was measured with a spring scale, to the nearest 0.25-gram. I continued to monitor the nests until after the juveniles fledged, so that the final reproductive success of each individual could be determined for that season.

Blood Parasite Analysis

Immediately after collection of the blood sample, I transferred a 1-centimeter dot of blood to a clean, ungreased microscope slide, and pulled it with another clean slide to make a thin blood smear (Schall n.d., Houwen 2000, DeGroote & Rodewald 2008). The slides were allowed to air-dry and then were placed into a box for transport.

Back in the lab, I first fixed the slides by soaking them for one minute in pure methanol. Then, I stained the slides in Sigma-Aldrich Wright-Giemsa stain for one minute and soaked them in deionized water for four minutes. Each slide was then thoroughly rinsed in deionized water and left to air-dry on a slant (Sigma-Aldrich Protocol).

Later, the blood slides were each scanned for fifteen minutes using light microscopy under 1000x oil immersion for the presence of parasites (Kirkpatrick & Suthers 1988, Makler *et al* 1998, Webb *et al* 2005,). The genus of each parasite was determined with the help of Hawkey *et al* (1989). Even though this method can only detect acute, active infections that have not gone into remission, it is the fastest and most

reliable method barring dissecting the bird or inoculating a lab specimen (Herman 1938, Love *et al* 1953, Barnard *et al* 2010, Knutie *et al* 2013).

Hybrid Frequency Estimation

In order to calculate frequency of hybridization, I used two different methods to assign individuals to one of three different categories: pure Carolina chickadee, pure black-capped chickadee, or hybrid chickadee. First, a field technique was used that compares the length of the un-flattened wing chord (y) to the length of the tail (x; Yunick 2003). Any individuals falling to the left of the line specified by the equation y=2.20x-64 were putatively categorized as Carolina chickadees, while any individuals to the right of the line were putatively categorized as black-capped chickadees.

In addition, I used genotypes at seven microsatellite markers to determine species using STRUCTURE. This analysis was based on the 134 adult blood samples collected during 2013 and 2014 from breeding adults in four local study sites (Fig. 2, Tab. 1), and from an additional nine adults captured at Jacobsburg State Park outside of the breeding season. Additionally, to insure that genotypes from pure Carolina and black-capped chickadees were included, I obtained tissues from museums of specimens captured farther away from the hybrid zone, in Florida, Louisiana, northern Pennsylvania, and New York. DNA was extracted from the whole blood samples using a DNeasy Tissue Kit (Qiagen, Valencia, CA) by following the manufacturer's protocol, and from the tissue samples using a standard phenol-chloroform extraction method. I amplified and genotyped seven previously published microsatellite markers (Reudink *et al* 2005) using the published polymerase chain reaction (PCR) conditions, modified as described in

Appendix II. I first used the program STRUCTURE version 2.3.2 (Pritchard *et al* 2000, Falush *et al* 2003, Hubisz *et al* 2009) to estimate the most likely number of genetic clusters (K) present in my data. For 20 replicate runs at each K ranging from 1 to 12, I ran STRUCTURE for 100,000 steps after a burn-in of 200,000 steps. The admixture model with allele frequencies correlated among populations was used. Furthermore, sampling location was used as a prior (Hubisz *et al* 2009). Some of the preliminary runs showed variable estimates of alpha, so I followed the STRUCTURE manual and increased the SD of Proposal to update alpha to 0.075. STRUCTURE Harvester (Earl & vonHoldt 2012) analyzed the combined results and determined the most likely K value for the dataset using the method of Evanno et al (2005). As predicted, the most likely K equaled 2, corresponding to the two chickadee species (Tab. 2). Once it was determined that two was the most likely number of clusters, I did another, longer run of STRUCTURE with K=2 to estimate the ancestry of individuals from each population location. STRUCTURE ran for 1,000,000 steps after a burn-in of 1,500,000 steps, with the same settings detailed above to get my final species distribution.

Habitat Analysis

In order to determine whether specific environmental variables predicted the occurrence of nest competition, hybridization, or parasitism, I conducted a habitat analysis by quantifying the vegetation surrounding the artificial nests. I established a 10-meter radius circular plot around each artificial nest site and used standard forestry techniques to quantify vegetation following the methods of Mahon *et al* (2007 & 2008). I plotted the location, species, and diameter at breast height (DBH) for each tree and semi-

quantitatively described the understory vegetation by abundance (Cottam & Curtis 1956). In addition, the species and the distance of the closest trees in each plot were noted. Using the CI-110/CI-120 digital plant canopy imager (CID Inc., Camas, WA, USA) I took a picture of the canopy from the center of each plot, aligned to magnetic north, so leaf area index (LAI) could be calculated. Later, by adjusting the contrast and colors of the image, I accurately calculated LAI on CID Biosciences Inc. software version 5.3.3.1281 (CID 2014). Finally, the amount of damaged, infected, and dead trees was noted (Mahon *et al* 2008).

Data Analysis

All statistical analyses were performed using R version 3.1.1 (R Core Team 2014) with the nlme (Pinheiro *et al* 2014) and AICcmodavg (Mazerolle 2015) packages installed.

Reproductive success was characterized by the number of chicks fledged from each nest. I used linear models to test whether parasite infection status or habitat characteristics significantly affected the number of chicks fledged (Appendix III). Models were simplified by removing non-significant terms one-by-one, and verified by likelihood ratio tests and corrected Akaike information criterion (AICc) values.

I modeled probability of house wren takeover with a logistic regression analysis for the two breeding seasons. A generalized linear model (binomial distribution, logit link) was used with a binary response variable indicating whether each chickadee nest start was taken over by house wrens. The full model included the predictor variables of location, total DBH, number of trees per $100m^2$, LAI, average understory vegetation, the

interaction between LAI and clutch size, as well as lay date and clutch size as covariates. Model simplification included removing non-significant terms one by one, and each removal was verified using likelihood ratio tests and AICc values (Appendix IV).

The total number of positive blood smears for each study site was counted to determine the number of birds infected. A Pearson's chi-squared test was used to determine whether the sites differed in the prevalence of parasite infection (Appendix V). P-values for the chi-squared test were computed by Monte Carlo simulation with 2000 replicates. Since blood collection at Jacobsburg occurred outside of the breeding season and were of a different species (see Results, *Hybrid Frequency Estimation*), those birds were not included in this analysis. Adults and chicks were tested separately for differences among sites in the prevalence of parasite infection.

I used a linear mixed effects model to test for effects of parasite infection on both adult and chick condition. Condition was calculated separately for adults and chicks by extracting the residuals from linear regressions of mass on tarsus length, basically measuring body mass compared to bird size. The predictor variables in the adult model included fixed effects of parasite infection status, and covariates including location, brood size, hatch date, chicks fledged, sex, and various interactions, since they too could have an effect on condition. Individual nest ID was included as a random effect in each model. I used likelihood ratio tests and corrected AIC values to reduce each model by removing predictor variables one by one to get a best-fit model (Appendix VI). Next, a similar model for condition of chicks was run, which included the predictor variables parasites, location, number of siblings, hatch date, sex, and various interactions. Again, I accounted for shared environments by including nest ID as a random effect in the model.

Once more, non-significant terms were removed one by one using likelihood ratio tests and corrected AIC values (Appendix VII) to arrive at a best-fit model.

I tested for environmental predictors of reproductive success and parasite infection prevalence using the habitat data. For the habitat data I performed a non-metric multidimensional scaling (NMS) ordination to describe the dominant gradients of vegetation community composition and habitat quality using PC-ORD version 5.1 (MjM Software; McCune & Grace 2002). Correlations between vegetation community composition and variables related to chickadee health and fitness were explored.

Results:

Bird Capture and Nest Site Monitoring

In total, 304 birds were captured and released over the course of this study. I was able to follow 39 nests to completion. A summary of the breeding data by site can be seen in Table 1.

Reproductive success was not significantly influenced by any measured characteristics of the parent birds or the habitat surrounding each artificial snag (Tab. 3).

In total, house wrens destroyed 33% of the chickadee nest starts. When controlling for clutch size, the probability of house wren takeover tended to be higher when LAI was low. The best-fit model (lowest AICc) for the probability of house wren takeover was the model that included LAI and clutch size (Tab. 4, Fig. 3). Removing clutch size from the model resulted in a significant decrease in model fit and removing LAI from the model resulted in a model with borderline non-significant decrease in fit (Tab. 4). This suggests that clutch size and potentially LAI are important predictors of

house wren takeovers. This is supported by the fact that in the three models with similarly low AICc values, LAI was present in the two models with the lowest AICc, while clutch size is present in all three of these models. Thus, chickadees with nests in more open areas had a higher risk of nest takeover. There was a higher probability of takeover when there was a smaller clutch in the nest, which most likely indicates that house wrens were more likely to successfully take over recently established and incomplete chickadee nests.

Blood Parasite Analysis

Of the 183 blood samples examined for parasites, 28 were positive for parasite infection. Of these, 21 were collected from juveniles, while the remaining 7 were from adults. The parasite types included *Leucocytozoon*, *Trypanosoma*, *Plasmodium*, *Haemoproteus*, and some microfilariae. Blood parasites were detected in approximately 15% of the samples from each site, with no significant difference in parasite infection prevalence between sites (adults: X^2= 0.915 p= 0.925, chicks: X^2= 5.921 p= 0.102). A summary of the blood parasite raw data can be seen in Table 5.

Parasite infection did not affect adult condition. Parasites were not included in the best-fit model of adult condition (Tab. 6).

The best-fit model of chick condition included parasites (Tab. 7). The presence of parasites led to a significant decrease in chick condition by 0.339 ± 0.160 (p=0.037). Two models were relatively close in AICc values (delta AICc < 2), so I chose the one with the fewest number of parameters as the best-fit model, giving us the minimum adequate model (Anderson & Burnham 2002). However, parasite presence was the only

variable present in both of these models (Tab. 7), further supporting its effect on chick condition. Furthermore, parasite presence was not correlated with any of the measured habitat variables.

Hybrid Frequency Estimation

Based on the method from Yunick (2003), most of the birds captured were Carolina chickadees (Fig. 4). There were seven black-capped chickadees caught at Jacobsburg State Park, four from South Mountain, one from DeSales University, and two from Peace Valley Park. The two adults from Peace Valley were almost exactly on the line separating the two species. It is not possible to confidently diagnose hybrids using this method.

Using the seven microsatellite markers, I did not detect any hybridization between the Carolina chickadees and the black-capped chickadees in our local study sites. At Jacobsburg State Park, the population was purely black-capped chickadee, while everything from South Mountain and south was purely Carolina Chickadee (Fig. 5). The STRUCTURE plot in Figure 5 shows a clear break in genetic clusters between the South Mountain and Jacobsburg State Park sites, with no indication of hybrid individuals. However, putative hybrids were identified in the museum samples collected in Greene County, New York (Fig. 5). Of the fourteen individuals identified as black-capped chickadee by the Yunick (2003) method, only the seven collected from Jacobsburg State Park were confirmed to be genetically black-capped based on our STRUCTURE analysis. In contrast, all individuals identified as Carolina chickadee by the Yunick (2003) method

were confirmed to be genetically Carolina chickadee in the STRUCTURE analysis, with the exception of the two individuals from Jacobsburg State Park.

Habitat Analysis

A three-dimensional NMS ordination (final stress = 20.09) represented 71% of the variability in the vegetation species frequency data, and revealed differences in the vegetation communities among the different locations studied (Fig. 6). However, these differences were not strongly correlated with the various fitness and health measurements made on chickadees (Fig. 6, Tab. 8, Tab. 9). Ordinations using basal area and other aspects of forest structure, including tree density, understory vegetation, and number of dead trees, were also unrelated to chickadee health and fitness.

Discussion:

Bird Capture and Nest Site Monitoring

Reproductive success was not influenced by any of our measured variables. It is likely that number of chicks fledged per nest is due to an intricate combination of individual bird characteristics and habitat variables that we were not able to detect at this scale. In addition, since Carolina chickadees practice biparental care, the number of chicks fledged per nest could be more related to each parent bird's ability to care for their young than actual parent condition (Otter 2007).

House wrens had the biggest effect on the reproductive success of Carolina chickadees by destroying one third of the chickadee nests. When nests are taken over there is no chance for a new generation to continue that lineage. With little chance of a

nest restart, and only a two and a half year life-span, this can cut overall chickadee reproduction in half (Brewer 1963, White & Kennedy 1997). I found that as long as the chicks were able to hatch, almost all juveniles successfully fledged, consistent with previous studies saying chickadees are usually successful unless they are taken over by house wrens (Brewer 1963).

A higher chance of house wren takeover was correlated with a lower LAI, or a more open area (Tab. 4, Fig. 3). This is consistent with previous studies indicating that house wrens prefer habitat edges and less mature forests (White & Kennedy 1997, Doherty Jr. & Grubb Jr. 2002). It is unknown whether this relationship is because the nests are easier for house wrens to spot, or if they are just present in areas with a higher house wren population.

The appearance of clutch size in the models predicting house wren takeover is likely a covariate indicating what stage of nest building or egg laying the chickadees were in. Since a smaller clutch size correlated with a higher chance of house wren takeover, it is likely that house wrens strike when chickadees are in an earlier nest stage. This could also indicate that chickadees defend their nests more intensely when they are farther along in the breeding attempt.

Climate change has already been blamed for migratory and phenological changes in many different organisms, including birds (Walther *et al* 2002, Hoffman & Sgrò 2011, Chen *et al* 2011, Harmon & Barton 2013). It is reasonable to assume that both chickadees and house wrens are just as vulnerable to these changes. If chickadees and house wrens do not alter their breeding times at the same rate or house wren populations increase due to climate change, it is not known how the house wren threat to reproductive

success of chickadees will react (Chen *et al* 2011). To further understand how this interspecific interaction might progress, studies on house wren phenology will be necessary. Additional migratory and phenological changes may even put the chickadees in competition with additional species. Competition with European starlings has also been documented in the Seattle, Washington area (Blewett & Marzluff 2005), which may affect chickadee fitness.

Blood Parasite Analysis

The numbers calculated of Carolina chickadee adults infected with parasites is consistent with other, previous studies (Kirkpatrick & Suthers 1988, Stabler & Kitzmiller 1970, Garvin & Remsen 1997). To my knowledge, no other studies have looked at chick infections in this species, and our work provides important baseline information on parasite prevalence at this life stage.

The presence of blood parasites in adult chickadees did not affect adult condition. Several possibilities may explain the lack of clear parasite effects on adult birds. The data could be skewed if I could not detect all of the infections with this method, if severely infected adults were not able to form breeding pairs at all, or if these specific parasites are not actually detrimental to their hosts. It is possible that I was just not able to detect a chronic infection in the adults if parasites were only present in low densities. This would have resulted in an individual considered a false negative with an abnormally lower condition. Furthermore, it is known that some species of parasites go into remission during the wintering period, and may not have re-emerged into the peripheral bloodstream in high enough densities yet to be detected (Herman 1938, Barnard & Bair

1986). Additionally, some species of parasites will only appear in the bloodstream of their host at night (Robinson Jr. 1961). If it is a recent infection, it can take up to four weeks to show up in the peripheral blood smears (Knowles *et* al 2009, Knutie *et al* 2013). Moreover, it is possible that adults that are severely infected with blood parasites are not even able to form a breeding pair since they are in such poor condition, have restricted movement, or not able to migrate (Ashgar *et al* 2011, Elahi *et al* 2014). If I had sampled the entire population of birds, instead of just the breeding pairs, it is possible that there would have been a higher infection rate. Finally, it has always been assumed that parasites have reduced the fitness of their host, but this assumption has been very rarely supported with data. It is always possible that these specific blood parasites ultimately do not have an effect on adult fitness since wild birds have coevolved with their parasites (Bennett *et al* 1988, Knowles *et al* 2009, Barnard *et al* 2010). Chronic infections do not always have negative side effects (Knowles *et al* 2009). Further research is necessary to determine which combination of explanations is most probable.

In contrast, the presence of blood parasites results in a lower condition for the chicks and it may have far reaching fitness effects. Parasite infection of nestling Carolina chickadees resulted in a significant decrease in condition (Tab. 7). Condition is a predictor of overall quality, and is positively correlated with larger and better offspring (Guillemain *et al* 2013). In other studies, it has been demonstrated that reduced condition in a chick may lead to a lower reproductive success since they are at a competitive disadvantage and have an overall lower condition (Medeiros & Freed 2009, Guillemain *et al* 2013). It has been shown in some studies that chicks with a higher mass typically become larger adults since they are better able to compete for food, store nutrients, and

deal with weather changes (Medeiros & Freed 2009). Having a better body condition during the first winter may give the chick a survival advantage and increase breeding success through a higher probability of mate attraction (Bennett *et al* 1988, Medeiros & Freed 2009, Grava *et al* 2013, Guillemain *et al* 2013). Chicks may not have a strong enough immune system to properly fend off parasites (Knutie *et al* 2013) especially in this very acute stage of the infection. It is unknown whether chick condition will decrease further with prolonged infection, or if they will be able to recover.

Hybrid Frequency Estimation

Surprisingly, there was no evidence of hybrid individuals at any of our sites. The population of chickadees at Jacobsburg State Park was pure black-capped chickadees, but anything south was pure Carolina chickadee with no hybrids present. The comparison of wing chord and tail length corroborated the DNA results. The wing chord and tail length measurements misidentified several individuals, but that is to be expected with size variations in any organism (Yunick 2003). Taylor *et al* (2014a) found hybrids as close as Hawk Mountain, which is only about 50-kilometers away from South Mountain. Other studies have also found hybrids (Reudink *et al* 2007) and demonstrated that the zone of contact is moving northward at a very rapid pace (Taylor *et al* 2014a). It is possible that the ecological constraints of the area or some other influence are allowing the Carolina chickadees to fully displace the black-capped chickadees instead of hybridizing. This data demonstrates the spatial heterogeneity of these processes along range margins and how little is actually understood. This goes to show that expected interspecific interactions might actually be more intricate then previously thought.

If Carolina chickadees are becoming the dominant species during these interactions, it is possible that their continued movement northward will eventually impact the fitness of the black-capped chickadees (Focht *et al* 2013). If coldest winter temperatures are the only parameter holding back Carolina chickadees from their shift northward, that could quickly alter with climate change (Taylor *et* al 2014a, McQuillan & Rice*, in review*). Character displacement may not have occurred yet if this sympatry is recent in evolutionary history, increasing the competition between the two species (Focht *et al* 2013). Even if the outcome of this competitive relationship proves to be beneficial for the Carolina chickadees, additional, potentially cascading interactions have not been assessed. An increased chance of hybridization is expected with many other species as ranges continue to move (Hoffman & Sgrò 2011).

Habitat Analysis

The habitat variables measured for each artificial nest site did not have any effect on reproductive success or parasite presence of the Carolina chickadees. It is possible that the scale they were measured on was too small to see any influences, and that the chickadees rely on stand level or forest level variations (Blewett & Marzluff 2005, Mahon *et al* 2007). Certainly aspects of forest structure, particularly LAI, did influence the probability of house wren takeover; however, LAI is not directly related to basal area or differences in species composition. Furthermore, other factors such as competition or predation may have a stronger influence on reproductive success than habitat variables (Zhu *et al* 2003, Zanette *et al* 2012).

General Conclusions

In my study, I was able to document some of the aspects of interspecific relationships that affect the fitness of Carolina chickadees. More work still needs to be done to examine potential synergistic effects or trophic cascades that may result from these seemingly insignificant interactions (Şekercioğlu *et al* 2012). This additional work should expand interspecific interactions as far as possible to include ecological responses of other organisms and how these interactions may feedback on the reproductive success of Carolina chickadees (Zhu *et al* 2012).

Chickadee ranges are expected to continue moving in the coming years (McQuillan & Rice, *in review*) and it is expected that many other species will also shift ranges due to climate change (Vallin *et al* 2012). Interspecific interactions will potentially be affected by range shifts and phenological changes in response to global change (Lavergne *et al* 2010, Dawson *et al* 2011). Even though Carolina chickadees may be of least concern to conservationists at the moment, they may become threatened due to synergistic affects of climate change with other ecological responses. Furthermore, it is possible that Carolina chickadees may actually become a threat to other species, if they are able to respond to climate change.

If scientists are to fully understand the impacts that changing climate has on our planet, species-level ecological responses must be better characterized, especially since not all species will respond in the same way (Vallin *et al* 2011, Chen *et al* 2011) and these responses will likely impact broader changes in the ecosystem and the critical services they provide. Models need to start including these types of species interactions and how they may be altered by climate change (Moss *et al* 2010, Hoffman & Sgrò 2011,

Şekercioğlu *et al* 2012). More baseline data of species interactions, as provided here, is necessary. If the possibilities of synergistic interspecific changes are not taken into account, small changes that may be overlooked may end up causing a much bigger cascade of consequences than originally thought. With so many expected changes in species distribution, phenologies, and parasite vector abundance, understanding ecological response is crucial to our overall knowledge of global change. Understanding the cumulative effects of interspecific interactions on the fitness of populations will likely facilitate improved predictions of ecological responses to changes in climate.

Table 1: Summary of bird capture and monitoring listed for each site. There were no snags set out for Jacobsburg State Park, only winter bird capture. JB, Jacobsburg State Park; SM, South Mountain; DS, DeSales University; NX, Nockamixon State Park; PV, Peace Valley Park.

Study Site	Year	Snags set out	Chickadee nests started	Chickadee nests completed	House wren nests	House wren nest takeovers	Chickadees captured
JB	2014	N/A	N/A	N/A	N/A	N/A	9
SM	2013	49	21	13	7	6	103
SM	2014	58	15	5	38	10	31
DS	2013	26	5	2	4	2	8
DS	2014	26	2	1	16	0	11
NX	2014	31	14	11	0	3	77
PV	2014	13	9	7	1	2	65

Table 2: STRUCTURE output for different assumed numbers of genetic clusters (K) present in the microsatellite data. The most likely number of clusters is two, bolded, and corresponds to the highest value of delta K.

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	20	-3819.345	0.7163	NA	NA	NA
2	**20**	**-3791.940**	**10.485**	**27.405**	**61.750**	**5.889**
3	20	-3826.285	29.833	-34.345	18.355	0.615
4	20	-3842.275	50.210	-15.990	11.105	0.221
5	20	-3847.160	42.878	-4.885	8.715	0.203
6	20	-3843.330	40.905	3.830	10.205	0.249
7	20	-3829.295	52.114	14.035	12.430	0.239
8	20	-3827.690	37.481	1.605	0.785	0.021
9	20	-3826.870	32.463	0.820	11.210	0.345
10	20	-3837.260	32.695	-10.390	18.610	0.569
11	20	-3829.040	37.835	8.220	33.620	0.889
12	20	-3854.440	98.880	-25.400	NA	NA

Table 3: Tests for the effects of parasite infection, condition, location, and other covariates on overall reproductive success measured by number of chicks fledged. The fixed effects included in each model, the AICc, and the likelihood ratio is listed for each model. The P-value corresponds to a likelihood ratio test comparing the fit of each model to the model directly above ($P > 0.05$ validates model simplification). There was no model with significant fixed effects.

Model	AICc	Likelihood Ratio	P-value
Lay Date + Parasites + Condition + Lay Date:Parasites + Condition:Parasites	233.318		
Lay Date + Parasites + Condition + Lay Date:Parasites	231.032	1.913	0.539
Lay Date + Parasites + Condition	230.774	10.739	0.143
Parasites + Condition	228.420	0.567	0.740
Condition	226.216	0.776	0.694
Avg. Veg. + Veg. Score + Total DBH + Trees/100m^2 + LAI	184.206		
Veg. Score + Total DBH + Trees/100m^2 + LAI	181.218	0.001	0.991
Total DBH + Trees/100m^2 + LAI	178.486	0.3134	0.799
Trees/100m^2 + LAI	175.899	0.231	0.824
Trees/100m^2	174.407	4.259	0.334

Table 4: Tests for effects of environmental variables on the probability of chickadee nest takeovers by house wrens. The fixed effects included in each logistic regression, the AICc, and the likelihood ratio is listed for each model. The p-value corresponds to a likelihood ratio test comparing the fit of each model to the model directly above, except where noted ($P > 0.05$ validates model simplification). The bolded model indicates the best-fit model, with the lowest AICc.

Model	AICc	Likelihood Ratio	P-value
Lay Date + Location + Total DBH + Trees/100m^2 + LAI + Clutch Size + LAI:Clutch Size + Avg. Veg.	71.020		
Lay Date + Total DBH + Trees/100m^2 + LAI + Clutch Size + LAI:Clutch Size + Avg. Veg.	63.207	1.353	0.717
Total DBH + Trees/100m^2 + LAI + Clutch Size + LAI:Clutch Size + Avg. Veg.	60.428	0.005	0.943
Total DBH + Trees/100m^2 + LAI + Clutch Size + Avg. Veg.	57.831	0.066	0.797
Total DBH + LAI + Clutch Size + Avg. Veg.	55.371	0.089	0.765
Total DBH + LAI + Clutch Size	53.066	0.139	0.710
LAI + Clutch Size	**52.131**	**1.408**	**0.235**
LAI	61.009	11.128	0.001
Clutch Size[a]	53.379	7.630	0.061

[a]P-value corresponds to likelihood ratio test comparing this model to the model including LAI and Clutch Size as fixed effects.

Table 5: Summary of parasite infections by location, age, and parasite genus. These data were only collected for the 2014-breeding season, not including the birds collected during the winter in Jacobsburg State Park. Due to mixed infections, the parasite genus may not exactly match the number of positive birds. AHY, after hatch year adult; JUV, 10 day-old juvenile chick. L, *Leucocytozoon*; T, *Trypanosoma*; P, *Plasmodium*; H, *Haemoproteus*; M, microfilariae.

Study Sites	# Birds Examined (AHY, JUV)	# Birds Positive (AHY, JUV)	% Birds Positive (AHY, JUV)	Parasites				
				L	T	P	H	M
SM	14, 17	2, 5	14%, 29%	2	1	1	2	2
DS	4, 7	0, 1	0%, 14%	1	0	0	0	0
NX	20, 56	3, 12	15%, 21%	2	1	5	2	6
PV	21, 44	2, 3	10%, 15%	0	1	1	0	3

Table 6: Tests for the effects of parasite infection and other covariates on adult condition. The fixed effects included in each model, the AICc, and the likelihood ratio is listed for each model. The P-value corresponds to a likelihood ratio test comparing the fit of each model to the model directly above (P > 0.05 validates model simplification). The bolded model indicates the best-fit model, with the lowest AICc.

Model	AICc	Likelihood Ratio	P-value
Parasites + Location + Brood Size + Hatch Date + Parasites:Hatch Date + Location:Hatch Date + Brood Size:Hatch Date + Chicks Fledged + Sex	106.625		
Parasites + Location + Brood Size + Hatch Date + Parasites:Hatch Date + Brood Size:Hatch Date + Chicks Fledged + Sex	94.478	0.227	0.973
Parasites + Location + Brood Size + Hatch Date + Parasites:Hatch Date + Chicks Fledged + Sex	90.852	0.053	0.818
Parasites + Location + Brood Size + Hatch Date + Chicks Fledged + Sex	87.484	0.117	0.733
Parasites + Location + Brood Size + Hatch Date + Sex	84.185	0.007	0.932
Location + Brood Size + Hatch Date + Sex	81.675	0.631	0.427
Location + Hatch Date + Brood Size	79.985	1.298	0.255
Location + Hatch Date	**78.686**	**1.547**	**0.214**
Hatch Date	79.428	8.519	0.036

Table 7: Tests for the effects of parasite infection and other covariates on 10 day-old chick condition. The fixed effects included in each model, the AICc, and the likelihood ratio is listed for each model. The P-value corresponds to a likelihood ratio test comparing the fit of each model to the model directly above ($P > 0.05$ validates model simplification). The bolded model indicates the best-fit model, with the lowest AICc.

Model	AICc	Likelihood Ratio	P-value
Parasites + Location + Number Siblings + Hatch Date + Parasites:Location + Parasites:Hatch Date + Location:Hatch Date + Number Siblings:Hatch Date + Sex	242.886		
Parasites + Location + Number Siblings + Hatch Date + Parasites:Location + Parasites:Hatch Date + Location:Hatch Date + Sex	239.958	<0.001	0.996
Parasites + Location + Hatch Date + Parasites:Location + Parasites:Hatch Date + Location:Hatch Date + Sex	237.236	0.142	0.706
Parasites + Location + Hatch Date + Parasites:Hatch Date + Location:Hatch Date + Sex	230.071	1.066	0.785
Parasites + Location + Hatch Date + Location:Hatch Date + Sex	227.663	0.222	0.638
Parasites + Location + Hatch Date + Sex	225.618	5.524	0.137
Parasites + Location + Sex	223.231	0.035	0.851
Parasites + Sex	220.335	4.089	0.252
Parasites	**220.320**	**4.420**	**0.110**
Sex[b]	222.461	4.365	0.037

[b]P-value corresponds to likelihood ratio test comparing this model to the model including Parasites and Sex as fixed effects.

Table 8: The NMS ordination results of a matrix with various reproductive success parameters laid over a matrix of the tree species frequency for all sites used by chickadees. Any tree species appearing less than five times in total was removed from the analysis. Pearson and Kendall correlations with ordination axes N=58.

Axis:	**1**	**2**	**3**
	r	r	r
Lay Date	0.104	0.102	-0.13
Clutch Size	0.052	0.04	0.259
Hatch Date	0.117	0.102	0.213
Brood Size	0.154	0.09	0.325
Hatch Success	0.207	0.106	0.295
Fledge Success	0.183	0.069	0.213
Chicks Fledged	0.146	0.059	0.305
Adult Condition	-0.146	0.226	0.07
Chick Condition	-0.173	0.067	-0.139
Parasite	0.174	0.235	-0.033

Table 9: The NMS ordination factor loading and characterization of variation results of the same matrix as Table 8. Any tree species appearing less than five times in total was removed from the analysis resulting in seventeen taxa used in the analysis. The full names of the tree species used can be seen in Appendix VIII.

Tree Species	**Axis 1**	**Axis 2**	**Axis 3**
Fraame	-0.209	0.038	0.333
Acespp	0.217	0.377	0.102
Quespp	0.074	-0.054	-0.264
Carspp	0.248	-0.013	-0.099
Hamvir	0.111	-0.402	-0.104
Betlen	-0.237	0.044	-0.345
Pruspp	-0.443	-0.332	-0.113
Lirtul	0.211	-0.267	-0.107
Sasalb	-0.645	-0.412	-0.336
Vibspp	-0.198	-0.374	0.199
Fagspp	-0.063	0.235	-0.493
Nyssyl	-0.294	-0.299	-0.109
Picspp	-0.049	0.068	-0.080
Corflo	0.125	0.035	-0.108
Ulmspp	0.244	0.430	0.328
Aesspp	0.551	-0.146	0.384
Dead	-0.143	0.250	0.006
% Variation Explained	**21.5%**	**33.3%**	**16.5%**

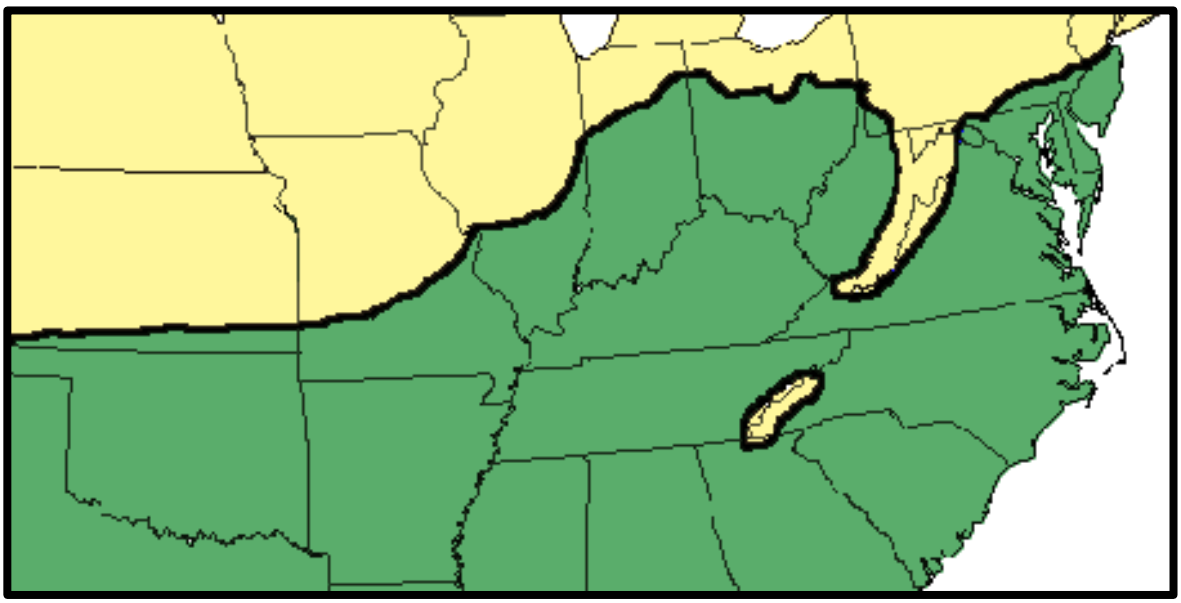

Figure 1: Published contact zone in 1999 between the Carolina chickadee (green) and black-capped chickadee (yellow) ranges (Kammermeier & Kelling 1999).

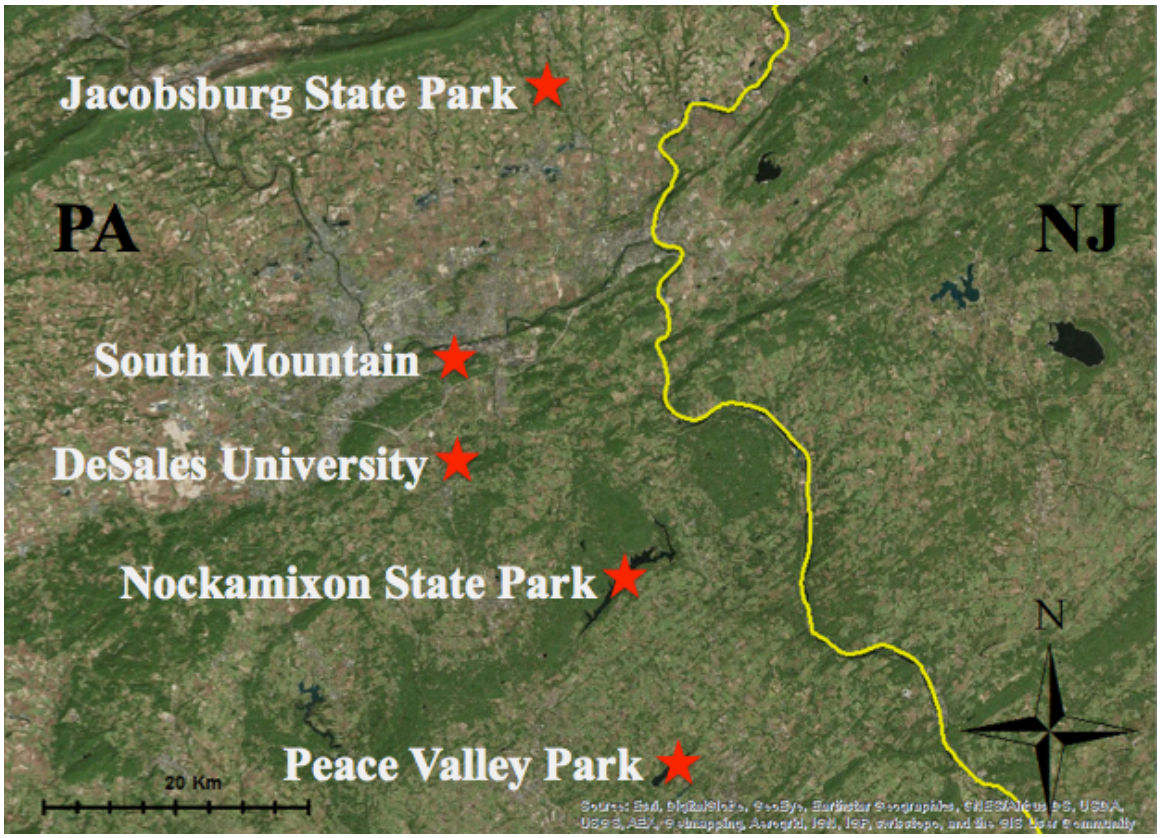

Figure 2: Overall map of the study sites on ArcGIS 10.1 with an Environmental Systems Research Institute air photo basemap of the area. The yellow line is the Delaware River, separating New Jersey from Pennsylvania. (ESRI 2014, Pennsylvania State University 2013).

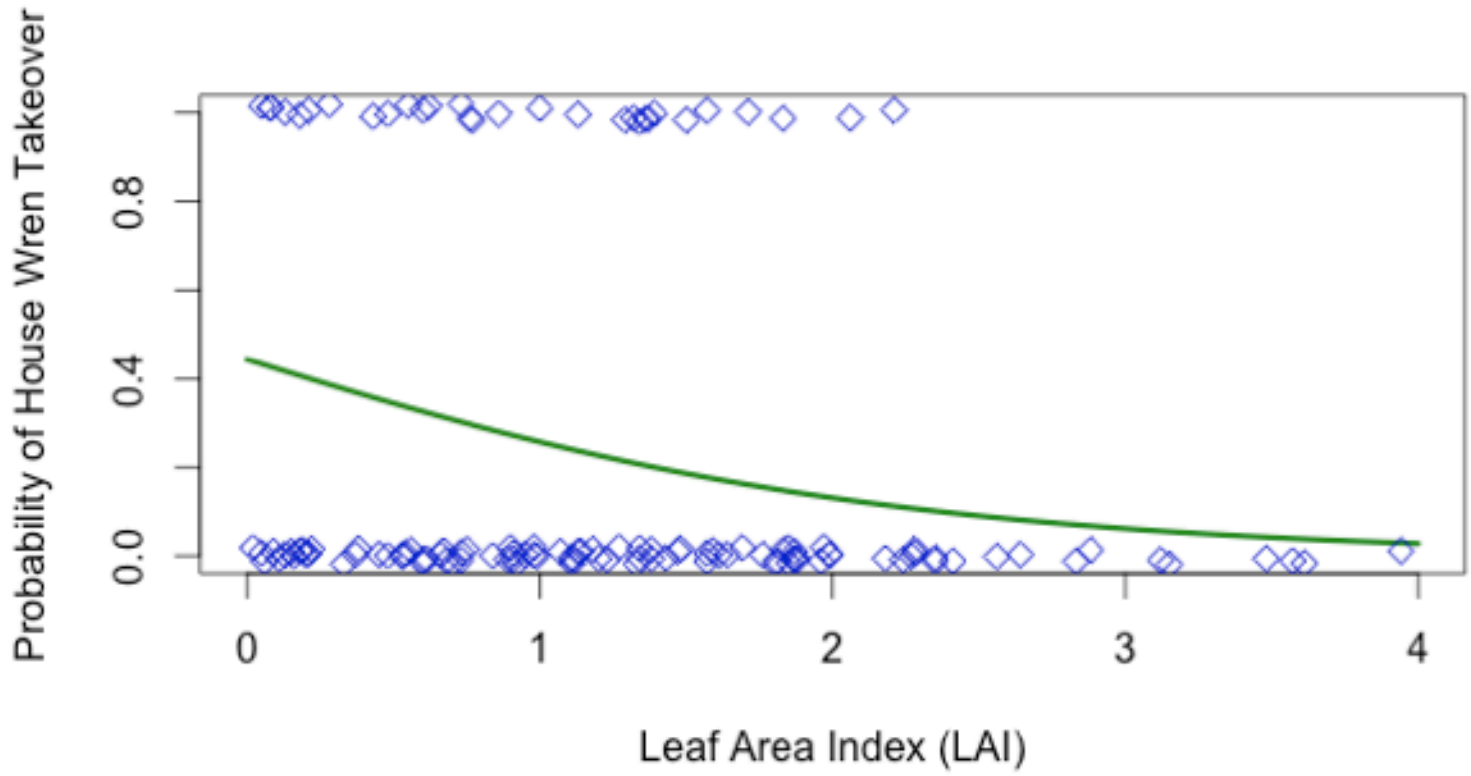

Figure 3: The predicted probability of house wren takeover of chickadee nest starts as a function of LAI. The clutch size was held constant at the mean clutch size, calculated as six eggs per nest. The blue diamonds represent the raw data points for all of the artificial nests that were used to make the logistical model. Jitter has been applied for illustrative purposes.

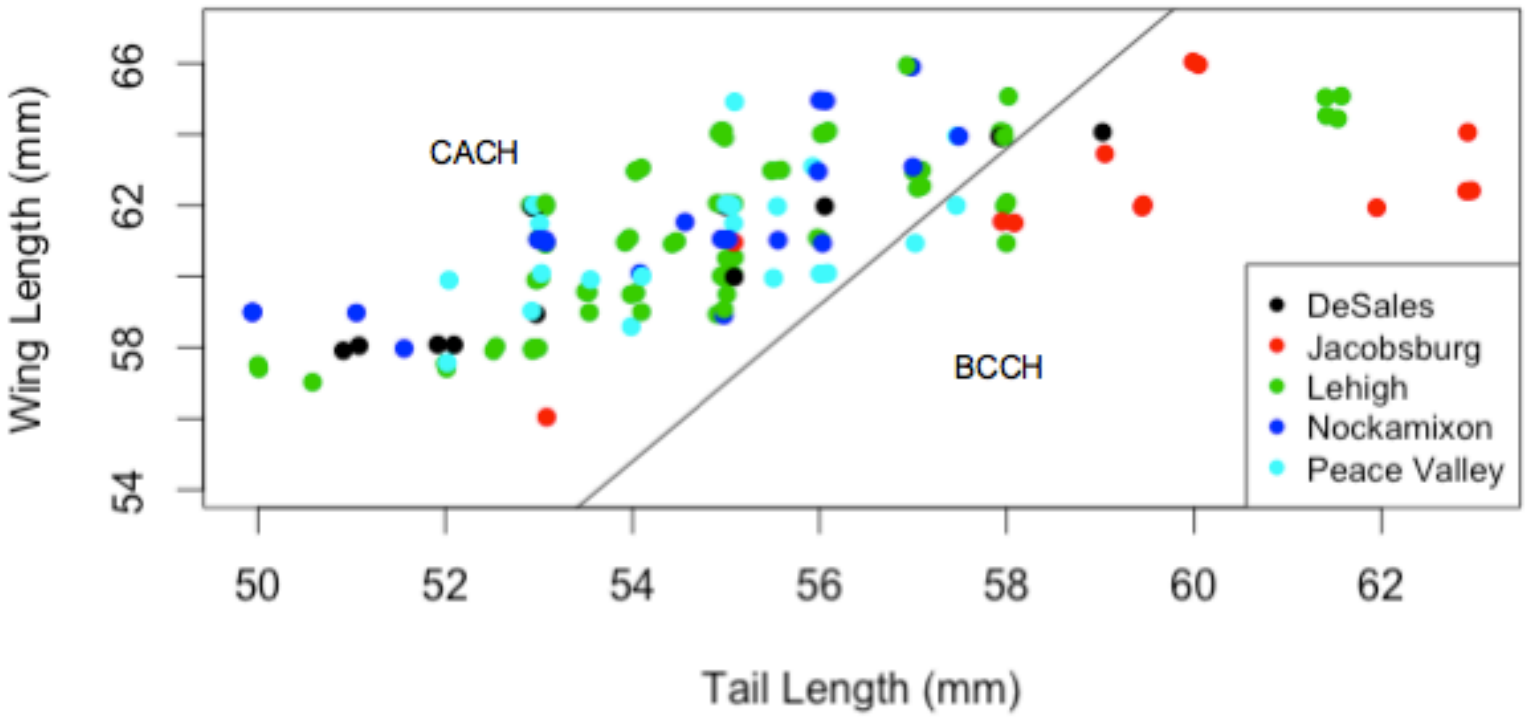

Figure 4: Wing chord length versus tail length measurements of each individual adult. The line is based on Yunick (2003), and is used for species identification of each individual. On the left side of the line are all individuals with measurements consistent with Carolina chickadees and on the right side of the line are all individuals with measurements consistent with black-capped chickadees. The colors indicate the location of capture for each individual (see legend). Jitter has been applied for illustrative purposes

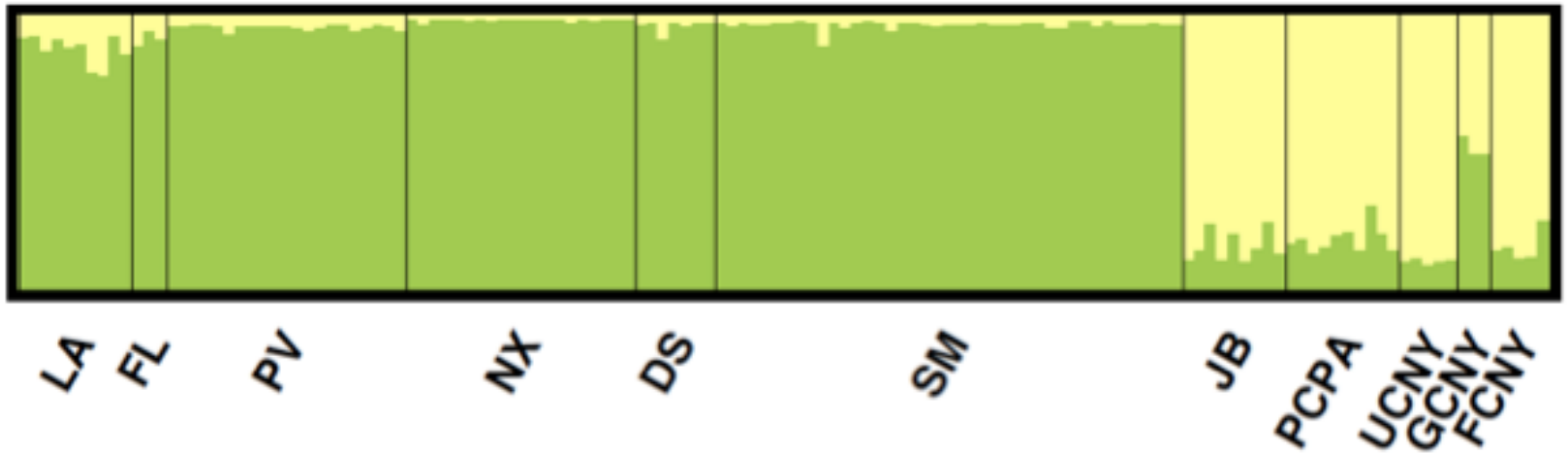

Figure 5: STRUCTURE membership assignment to genetic clusters based on microsatellite data, with two genetic clusters assumed. Each vertical bar represents membership assignment for one individual. The proportion of each color represents the posterior probability of assignment to each cluster. Green represents the cluster associated with Carolina chickadees, while yellow represents the cluster associated with black-capped chickadees. Study site locations are listed at the bottom, from south (left) to north (right). The only individuals likely to be hybrids were captured north of South Mountain, in Greene County, NY. LA, Louisiana; FL, Florida; PV, Peace Valley Park; NX, Nockamixon State Park; DS, DeSales University; SM, South Mountain; JB, Jacobsburg State Park; PCPA, Potter County, PA; UCNY, Ulster County, NY; GCNY, Greene County, NY; FCNY, Franklin County, NY.

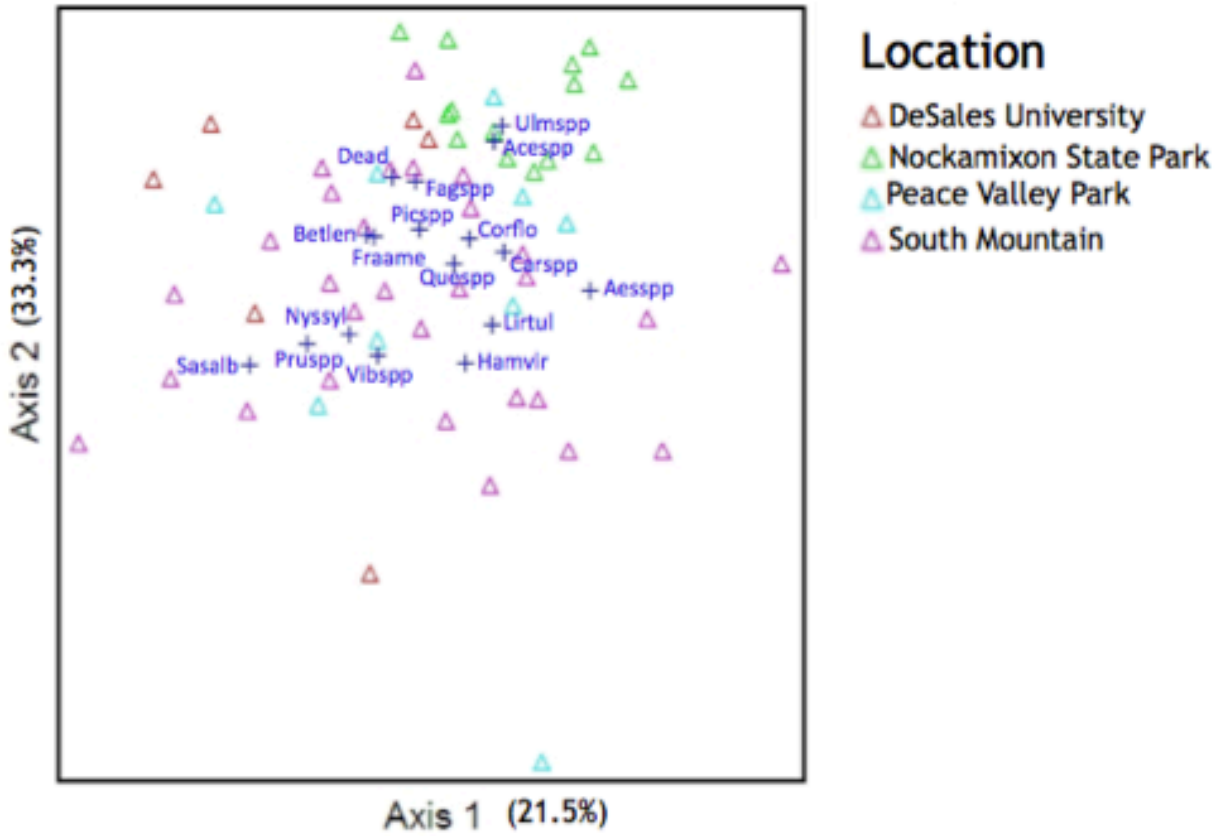

Figure 6: The NMS output graph of a matrix with location overlain over a matrix of the tree species frequency for all sites used by chickadees. Tree species are the labeled crosses, and the full names can be seen in Appendix VIII. Any species appearing less than five times was removed from the ordination. Although no strong trends were seen, clustering still appeared by location (see legend).

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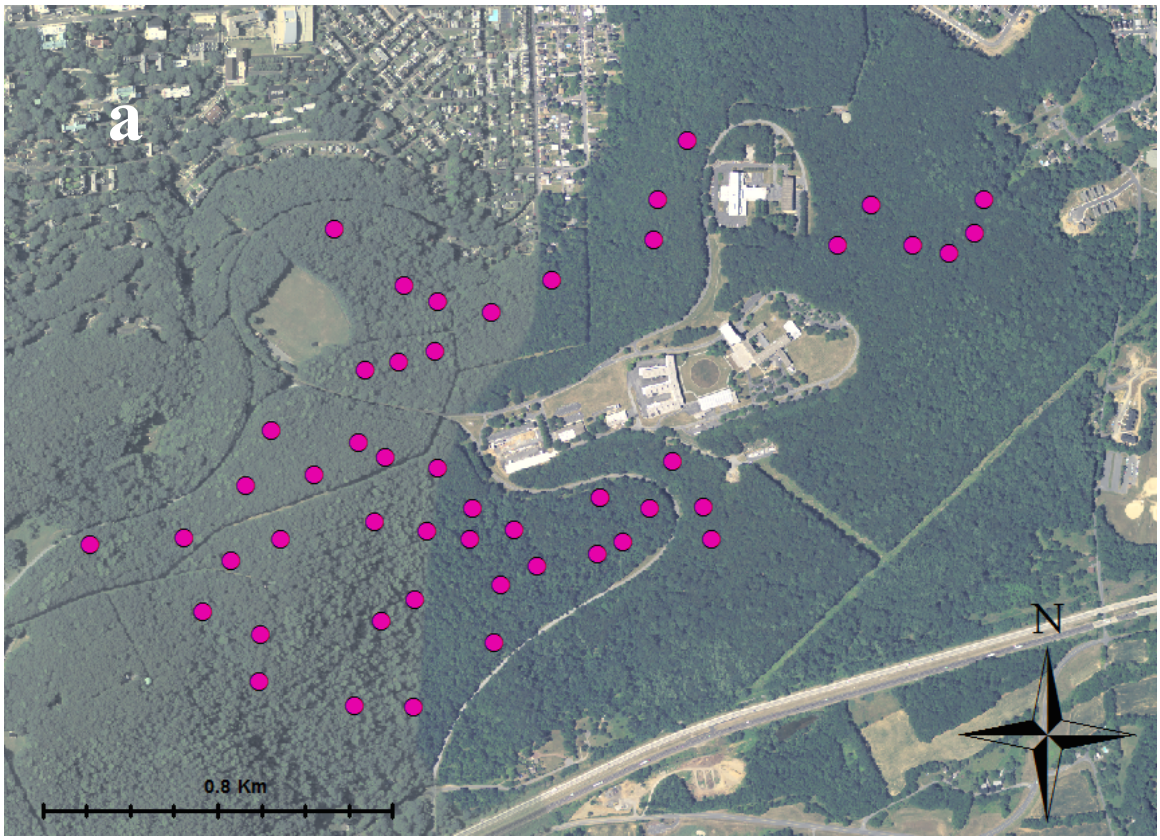
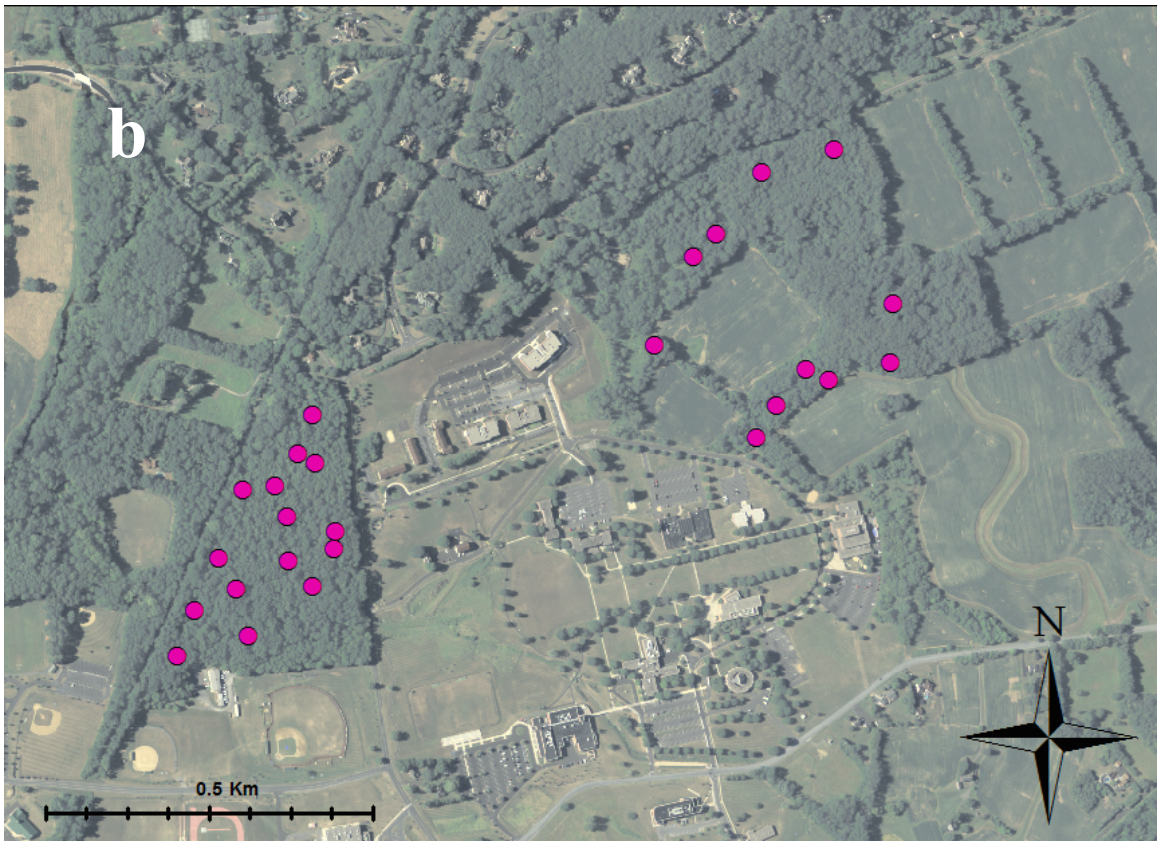
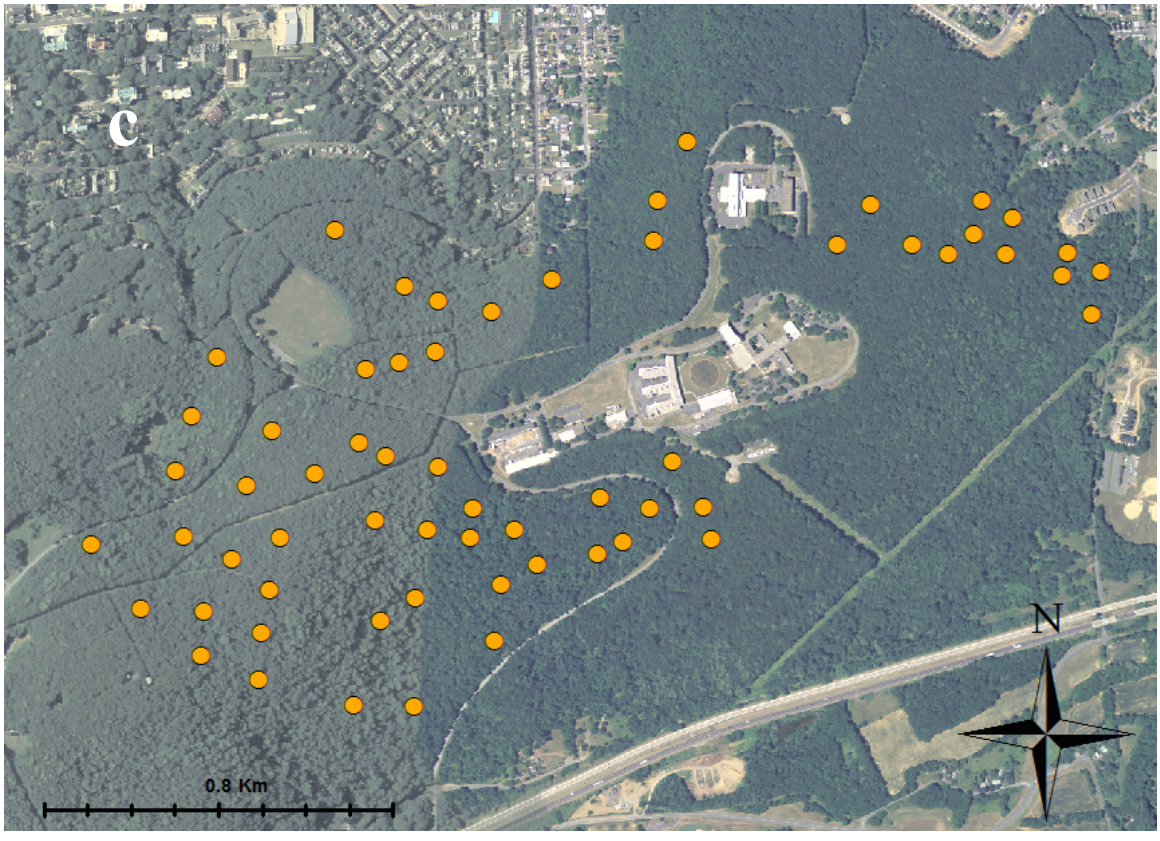
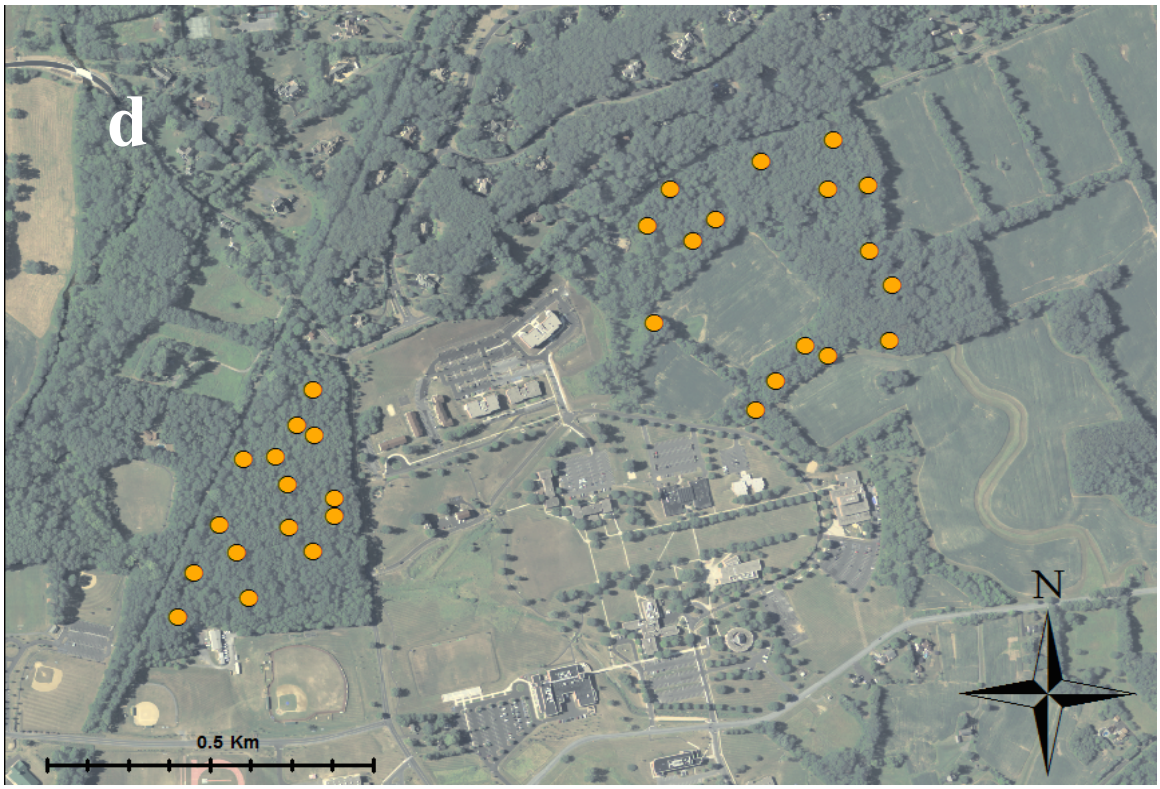
Appendix I: Maps of snags at each monitored location made in ArcGIS 10.1 with maps from Pennsylvania Spatial Data Analysis (PASDA; Pennsylvania State University 2013). For the 2013 breeding season, (a) is South Mountain and (b) is DeSales University. For the 2014 breeding season (c) is South Mountain, (d) is DeSales University, (e) is Nockamixon State Park, and (f) is Peace Valley Park.




b
N
0.5 Km


c
N
0.8 Km


d
0.5 Km
N


e
2 Km
N


f
1.1 Km
N

Appendix II: Optimized annealing temperatures for PCR for the microsatellites. The cycle parameters were 95°C for 3 minutes, 94°C for 30 seconds, T_a for 45 seconds, and 72°C for 45 seconds. This repeated 34 times, with an extension for 5 minutes, and finally holding at 4°C.

Microsatellite Marker	**Optimal Annealing Temperatures (T_a)(°C)**
Pca2	61.7
Pca4	55.8
Pca8	55.4
Pat2-14	43.5
Pat2-43	51.5
Titgata02	58
Titgata39	54

Appendix III: R code for linear model for overall reproductive success.

```
#Model for reproductive success with adult variables
ReproductiveSuccess <-
glm(Chicks_Fledged~Lay_Date+Parasites+Condition+Lay_Date:Parasites+Condition:Pa
rasites, data=Adults14, na.action=na.exclude)
summary(ReproductiveSuccess)
ReproductiveSuccess2 <-
glm(Chicks_Fledged~Lay_Date+Parasites+Condition+Lay_Date:Parasites,
data=Adults14, na.action=na.exclude)
summary(ReproductiveSuccess2)
anova(ReproductiveSuccess, ReproductiveSuccess2, test="Chisq")
ReproductiveSuccess3 <- glm(Chicks_Fledged~Lay_Date+Parasites+Condition,
data=Adults14, na.action=na.exclude)
summary(ReproductiveSuccess3)
anova(ReproductiveSuccess2, ReproductiveSuccess3, test="Chisq")
ReproductiveSuccess4 <- glm(Chicks_Fledged~Parasites+Condition, data=Adults14,
na.action=na.exclude)
summary(ReproductiveSuccess4)
anova(ReproductiveSuccess3, ReproductiveSuccess4, test="Chisq")
ReproductiveSuccess5 <- glm(Chicks_Fledged~Condition, data=Adults14,
na.action=na.exclude)
summary(ReproductiveSuccess5)
anova(ReproductiveSuccess4, ReproductiveSuccess5, test=”Chisq”)

#Model for reproductive success with habitat variables
RepSuccess <-
glm(ChicksFledged~Avg_Veg+Veg_Score+Total_DBH+Trees_100m2+LAI, data=Data)
summary(RepSuccess)
RepSuccess2 <- glm(ChicksFledged~Veg_Score+Total_DBH+Trees_100m2+LAI,
data=Data)
summary(RepSuccess2)
anova(RepSuccess, RepSuccess2, test="Chisq")
RepSuccess3 <- glm(ChicksFledged~Total_DBH+Trees_100m2+LAI, data=Data)
summary(RepSuccess3)
anova(RepSuccess2, RepSuccess3, test="Chisq")
RepSuccess4 <- glm(ChicksFledged~Trees_100m2+LAI, data=Data)
summary(RepSuccess4)
anova(RepSuccess3, RepSuccess4, test="Chisq")
RepSuccess5 <- glm(ChicksFledged~Trees_100m2, data=Data)
summary(RepSuccess5)
anova(RepSuccess4, RepSuccess5, test="Chisq")
```

Appendix IV: R code for generalized linear model for house wren takeovers.

```
#Making a model for logistics regression for HW takeovers for both years combined
based on different factors
HWTakeover <-
glm(HWTakeover~LayDate+Location+Total_DBH+Trees_100m2+LAI+ClutchSize+LA
I:ClutchSize+Avg_Veg, data=Data, family=binomial("logit"))
summary(HWTakeover)
drop1(HWTakeover, test="Chisq")
HWTakeover2 <-
glm(HWTakeover~LayDate+Total_DBH+Trees_100m2+LAI+ClutchSize+LAI:ClutchSi
ze+Avg_Veg, data=Data, family=binomial("logit"))
summary(HWTakeover2)
drop1(HWTakeover2, test="Chisq")
HWTakeover3 <-
glm(HWTakeover~Total_DBH+Trees_100m2+LAI+ClutchSize+LAI:ClutchSize+Avg_
Veg, data=Data, family=binomial("logit"))
summary(HWTakeover3)
drop1(HWTakeover3, test="Chisq")
HWTakeover4 <-
glm(HWTakeover~Total_DBH+Trees_100m2+LAI+ClutchSize+Avg_Veg, data=Data,
family=binomial("logit"))
summary(HWTakeover4)
drop1(HWTakeover4, test="Chisq")
HWTakeover5 <- glm(HWTakeover~Total_DBH+LAI+ClutchSize+Avg_Veg,
data=Data, family=binomial("logit"))
summary(HWTakeover5)
drop1(HWTakeover5, test="Chisq")
HWTakeover6 <- glm(HWTakeover~Total_DBH+LAI+ClutchSize, data=Data,
family=binomial("logit"))
summary(HWTakeover6)
drop1(HWTakeover6, test="Chisq")
HWTakeover7 <- glm(HWTakeover~LAI+ClutchSize, data=Data,
family=binomial("logit"))
summary(HWTakeover7)
drop1(HWTakeover7, test="Chisq")
anova(HWTakeover7, test="Chisq")
DataClutch <- subset(Data, ClutchSize!="NA")
HWTakeover8 <- glm(HWTakeover~LAI, data=DataClutch, family=binomial("logit"))
summary(HWTakeover8)
anova(HWTakeover8, test="Chisq")
HWTakeover9 <- glm(HWTakeover~ClutchSize, data=Data, family=binomial("logit"))
summary(HWTakeover9)
anova(HWTakeover9, test="Chisq")
```

Appendix V: R code for comparing parasite prevalence during breeding season in our four monitored locations.

```
#To compare Parasite occurrence across locations, need to do a Chi-square test.
NoJB_Adults <- subset(DataAdults, Location!="JB")
NoJB_Chicks <- subset(DataChicks, Location!="JB")
Adults_Tab <- table(NoJB_Adults$Location, NoJB_Adults$Parasites, exclude="JB")
Chicks_Tab <- table(NoJB_Chicks$Location, NoJB_Chicks$Parasites, exclude="JB")
chisq.test(NoJB_Adults$Location, NoJB_Adults$Parasites, simulate.p.value=TRUE)
chisq.test(NoJB_Chicks$Location, NoJB_Chicks$Parasites, simulate.p.value=TRUE)
prop.test(Adults_Tab[,"Yes"], margin.table(Adults_Tab,1))
prop.test(Chicks_Tab[,"Yes"], margin.table(Chicks_Tab,1))
```

Appendix VI: R code for the linear mixed effect model to determine what influenced variation in adult condition.

```
#Linear mixed effect model to determine what causes variation in adult condition
LMEAdultCondition <-
lme(Condition_Adults~Parasites+Location+Brood_Size+Hatch_Date+Parasites:Hatch_D
ate+Location:Hatch_Date+Brood_Size:Hatch_Date+Chicks_Fledged+Sex,
random=~1|Nest_ID, data=Adults14, na.action=na.exclude, method="ML")
summary(LMEAdultCondition)
LMEAdultCondition2 <-
lme(Condition_Adults~Parasites+Location+Brood_Size+Hatch_Date+Parasites:Hatch_D
ate+Brood_Size:Hatch_Date+Chicks_Fledged+Sex, random=~1|Nest_ID,
data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition, LMEAdultCondition2)
summary(LMEAdultCondition2)
LMEAdultCondition3 <-
lme(Condition_Adults~Parasites+Location+Brood_Size+Hatch_Date+Parasites:Hatch_D
ate+Chicks_Fledged+Sex, random=~1|Nest_ID, data=Adults14, na.action=na.exclude,
method="ML")
anova(LMEAdultCondition2, LMEAdultCondition)
summary(LMEAdultCondition3)
LMEAdultCondition4 <-
lme(Condition_Adults~Parasites+Location+Brood_Size+Hatch_Date+Chicks_Fledged+
Sex, random=~1|Nest_ID, data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition3, LMEAdultCondition4)
summary(LMEAdultCondition4)
LMEAdultCondition5 <-
lme(Condition_Adults~Parasites+Location+Brood_Size+Hatch_Date+Sex,
random=~1|Nest_ID, data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition4, LMEAdultCondition5)
summary(LMEAdultCondition5)
LMEAdultCondition6 <-
lme(Condition_Adults~Location+Brood_Size+Hatch_Date+Sex, random=~1|Nest_ID,
data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition5, LMEAdultCondition6)
summary(LMEAdultCondition6)
LMEAdultCondition7 <- lme(Condition_Adults~Location+Hatch_Date+Brood_Size,
random=~1|Nest_ID, data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition6, LMEAdultCondition7)
summary(LMEAdultCondition7)
LMEAdultCondition8 <- lme(Condition_Adults~Hatch_Date+Location,
random=~1|Nest_ID, data=Adults14, na.action=na.exclude, method="ML")
anova(LMEAdultCondition7, LMEAdultCondition8)
summary(LMEAdultCondition8)
LMEAdultCondition9 <- lme(Condition_Adults~Hatch_Date, random=~1|Nest_ID,
data=Adults14, na.action=na.exclude, method="ML")
```

```
summary(LMEAdultCondition9)
anova(LMEAdultCondition9, LMEAdultCondition8)
LMENullAdultCondition <- lme(Condition_Adults~1, random=~1|Nest_ID,
data=Adults14, na.action=na.exclude, method="ML")
summary(LMENullAdultCondition)
```

Appendix VII: R code for the linear mixed effect model to determine what influenced variation in chick condition.

```
#Linear mixed effect model to see if there is a significant difference with condition & parasites with chicks from 2014
LMEChickCondition <- lme(Condition_Chicks~Parasites+Location+Number_Siblings+Hatch_Date+Parasites:Location+Parasites:Hatch_Date+Location:Hatch_Date+Number_Siblings:Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
plot(LMEChickCondition)
summary(LMEChickCondition)
anova(LMEChickCondition)
LMEChickCondition2 <- lme(Condition_Chicks~Parasites+Location+Number_Siblings+Hatch_Date+Parasites:Location+Parasites:Hatch_Date+Location:Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
anova(LMEChickCondition, LMEChickCondition2)
summary(LMEChickCondition2)
anova(LMEChickCondition2)
LMEChickCondition3 <- lme(Condition_Chicks~Parasites+Location+Hatch_Date+Parasites:Location+Parasites:Hatch_Date+Location:Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
anova(LMEChickCondition2, LMEChickCondition3)
summary(LMEChickCondition3)
anova(LMEChickCondition3)
LMEChickCondition4 <- lme(Condition_Chicks~Parasites+Location+Hatch_Date+Parasites:Hatch_Date+Location:Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
anova(LMEChickCondition3, LMEChickCondition4)
summary(LMEChickCondition4)
anova(LMEChickCondition4)
LMEChickCondition5 <- lme(Condition_Chicks~Parasites+Location+Hatch_Date+Location:Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
anova(LMEChickCondition4, LMEChickCondition5)
summary(LMEChickCondition5)
anova(LMEChickCondition5)
LMEChickCondition6 <- lme(Condition_Chicks~Parasites+Location+Hatch_Date+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
summary(LMEChickCondition6)
anova(LMEChickCondition6)
anova(LMEChickCondition5, LMEChickCondition6)
LMEChickCondition7 <- lme(Condition_Chicks~Parasites+Location+Sex, random=~1|Nest_ID, data=Chick14, na.action=na.exclude, method="ML")
```

```
anova(LMEChickCondition6, LMEChickCondition7)
summary(LMEChickCondition7)
anova(LMEChickCondition7)
anova(LMEChickCondition7)
LMEChickCondition8 <- lme(Condition_Chicks~Parasites+Sex, random=~1|Nest_ID,
data=Chick14, na.action=na.exclude, method="ML")
summary(LMEChickCondition8)
anova(LMEChickCondition8)
anova(LMEChickCondition7, LMEChickCondition8)
LMEChickCondition9 <- lme(Condition_Chicks~Parasites, random=~1|Nest_ID,
data=Chick14, na.action=na.exclude, method="ML")
summary(LMEChickCondition9)
anova(LMEChickCondition8, LMEChickCondition9)
anova(LMEChickCondition9, test="Chisq")
LMEChickCondition10 <- lme(Condition_Chicks~Sex, random=~1|Nest_ID,
data=Chick14[c(1:16,18:41,43:84,86:113),], na.action=na.exclude, method="ML")
summary(LMEChickCondition10)
LMENullChickCondition <- lme(Condition_Chicks~1, random=~1|Nest_ID,
data=Chick14[c(1:16,18:41,43:84,86:113),], na.action=na.exclude, method="ML")
summary(LMENullChickCondition)
anova(LMEChickCondition8, LMENullChickCondition)
anova(LMEChickCondition9, LMENullChickCondition)
```

Appendix VIII: Species abbreviations used in the NMS ordination.

Species Abbreviations	Scientific Species Name	Common Species Name
Ulmspp	*Ulmus spp.*	Elm
Acespp	*Acer spp.*	Maple
Dead	-	All Dead Trees
Fagspp	*Fagus spp.*	Beech
Picspp	*Picea spp.*	Spruce
Betlen	*Betula lenta*	Black Birch
Corflo	*Cornus florida*	Flowering Dogwood
Fraame	*Fraxinus americanas*	White Ash
Carspp	*Carya spp.*	Hickory
Quespp	*Quercus spp.*	Oak
Aesspp	*Aesculus spp.*	Buckeye
Nyssyl	*Nyssa sylvatica*	Black Gum
Lirtul	*Liriodendron tulipfera*	Tulip Tree
Sasalb	*Sassafras albidum*	Sassafras
Pruspp	*Prunus spp.*	Cherry Tree
Vibspp	*Viburnum spp.*	Viburnum
Hamvir	*Hamamelis virginiana*	Witch Hazel

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Master of Science in Earth & Environmental Science, expected May 2015 (GPA: 3.92)
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Research Experience for Undergraduates in Ocean Sciences at the Rutgers University Marine Field Station, Tuckerton, NJ, (June-August 2013)
Internship with Bluestone Environmental Services, New Brunswick, NJ, (June-August 2012)
South Africa Study Abroad Program, Michigan State University, East Lansing, MI, (May-June 2012)

Selected Publications & Presentations

Navara, C. E., Rice, A. M., & Booth, R. K. "The effects of interspecific interactions on the reproductive success of Carolina chickadees (*Poecile carolinensis*)." Lehigh University Earth & Environmental Science Graduate Symposium, Lehigh University. 20 Feb. 2015.

Navara, C. E., Rice, A. M., & Booth, R. K. "Effects of hybridization and habitat choice on fitness of black-capped chickadees (*Poecile atricapillus*)" Lehigh Valley Ecology & Evolution Society Meeting, Cedar Crest College. 29 Mar. 2014. **First Place, Student Poster Presentation**

Navara, C. E., Lopez-Duarte, P., & Able, K. "Dispersal of American horseshoe crab (*Limulus polyphemus*) larvae." Research Internships in Ocean Sciences, Rutgers University. 9 Aug. 2013. **Second Place, Student Poster Presentation**

Scholarships, Awards, & Funding

Lehigh U. EES Department Research Grant, Farney Funding (Spring 2014) **$400**
Lehigh U. EES Department Research Grant, Farney Funding (Fall 2013) **$980**
Lehigh U. Presidential Scholarship (Spring 2014-Fall 2014) **Up to 15 credits a semester**
Donnell Foster-Hewett Award (Spring 2014) **$1,000**
Robert W. Blake Award (Fall 2011) **$1,000**
Phi Eta Sigma National Honor Society (Spring 2011)
Dean's List (All Undergraduate Semesters)